ON THE ANATOMY OF *TURRITELLA COMMUNIS*, Risso.

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PLATE VI.

Considerable interest has recently centred round the Turritellidæ on account of the suggested affinities between some of the members of this family and the extinct Murchisoniidæ. Mr. Marrat, of Liverpool, who was the first to draw attention to the resemblances between the two families, went so far as to suggest that certain living Turritellidæ more properly belonged to the genus *Murchisonia*. The study of these doubtful Turritellidæ has been further carried on by Miss Donald [1] in connection with her researches on the Murchisoniidæ.

The genus *Murchisonia* is universally regarded as referable to the Diotocardia, i.e. to the most primitive group of living Prosobranchs, whereas *Turritella* is known to belong to the Monotocardia, and consequently to be more specialized. If, however, the above authorities are correct in their surmise that these notched Turritellidæ are living representatives of the genus *Murchisonia*, then two questions arise, viz.: (1) is the family Turritellidæ a very primitive one, much more so than is generally supposed, and having affinities to the Diotocardia? or (2) are we including in the Turritellidæ two entirely distinct types, one of which, comprising the forms with a notched peristome, belongs to the Diotocardia, and the other to the Monotocardia?

To enable us to settle these questions, for we have no knowledge whatever of the anatomy of the notch-bearing *Turritellæ*, we should need a great deal of material, which is at present unobtainable. In order, however, to be prepared in the future for the study of these forms, it is necessary first of all to know something of the anatomy of a typical *Turritella*, and, as at present the information on this point is somewhat meagre, it has been deemed advisable to describe briefly the anatomy of *Turritella communis*, Risso.

The material for this investigation was collected by Mr. M. F. Woodward while working at the Marine Laboratory of the Royal Society of Dublin, then stationed at Inishbofin, co. Galway; further

[1] Quart. Journ. Geol. Soc., vol. xliii (1887), pp. 618 and 619; vol. liv (1898), pp. 45–72; Proc. Malac. Soc. London, ante, pp. 47–55.

material has also been obtained through the kindness of Mr. E. W. L. Holt, the naturalist in charge of that station. Mr. Woodward kindly placed the material at my disposal, and I am further indebted to him for much valuable assistance.

External Characters.—It will be unnecessary for me to do more than call attention to one or two points of interest in connection with the external characters of the animal, as they have already been fully described by other observers [2]. On the right side of the animal, in the cephalic region, two conspicuous folds or lobes [Fischer, 3] are present (Pl. VI, Fig. 1); the smaller of these is situated low down, and from its innervation I should consider it to be the remains of an epipodium (*ep.*). The larger fold lies immediately underneath the right tentacle, and is seen to be the continuation of a fleshy ridge bounding a well-marked groove, the nature of which I shall refer to later on. This fold may be termed the *genital flap* (*g.f.*). The snout is short and broad; on it are situated awl-shaped diverging tentacles; the eyes, slightly prominent, lie at the outer bases of the tentacles. The margin of the mantle is fringed, as in *Cerithium*, and is moreover furnished with numerous papillæ (Pl. VI, Fig. 2, *m.p.*), the longer ones having their edges fimbriated. The foot is very short, truncate in front, attenuated and obtuse behind, grooved beneath; the operculigerous lobe is simple. Three pedal glands are present. In the anterior region of the foot there is a slight transverse cleft lined by glandular cells, which pour their secretion into the cleft. In the posterior region there is a small median gland (*sole gland*), which opens by a short duct near the end of the sole. In addition to these median glands, there is an unpaired structure on the right side of the foot, situated just above the opereulum; this may be termed the *supraopercular gland*. These structures are of minute size, and were only to be made out by the examination of a series of longitudinal and transverse sections through the head and foot. The operculum is a horny, circular, multispiral plate, with a central nucleus and fimbriated edge; it closely resembles the opereulum of *Potamides*.

Internal Anatomy. — *The Alimentary Canal.* — The mouth is situated near the tip of the snout on its ventral surface; its lateral walls are furnished with a pair of horny jaws, composed of minute chitinous tesseræ. The buccal mass is fairly large; its muscular system and radula-cartilage are well developed. A moderately-sized radula-sac is present.

A pair of very small salivary glands are situated at the sides of the buccal mass near its junction with the œsophagus; they immediately overlie the buccal ganglia. The salivary ducts open into the posterior portion of the mouth. The total length of glands and ducts is only about two-thirds that of the buccal mass. A very long, narrow œsophagus (Pl. VI, Fig. 2, *œs.*) leads out of the buccal mass, and, running parallel with the columella muscle, underneath the genital groove (*g.g.*), reaches the stomach (*st.*), which it enters on the right side a little above the median constriction. The stomach is a fairly large structure, divided by a median constriction into two

chambers, the upper (posterior) one receiving the œsophagus and bile duct, the lower (anterior) one leading out into the intestine.

The intestine, after leaving the stomach, passes back underneath the œsophagus for a short distance, then, curving on itself, passes to the right side of the mantle, and, running parallel with the genital duct, enlarges to form a glandular-walled rectum, which opens into the anterior portion of the mantle-cavity. The liver is situated in the centre of the visceral mass, and is entirely surrounded by the genital gland; it pours its secretion into the stomach by means of a bile duct, which enters the posterior chamber close to the opening of the œsophagus.

Radula.—Since there is a considerable amount of variation in the radulæ of different species of *Turritella*, it will be of interest, for purposes of comparison, to give a brief description of those forms that have, up to the present, been investigated. In the majority of cases the radula is typically tænioglossate, having a formula of 2 : 1 : 1 : 1 : 2, each transverse row of teeth consisting of an unpaired median, with a single admedian, and two laterals on either side.

The radula of *Turritella communis*, Risso, has been described and figured by Sars [8] (p. 185, pl. vii, fig. 1). The median tooth is quadrangular in shape, the base being broad and straight, its triangular apex is reflexed, the margin being provided with a large central cusp bordered laterally by numerous smaller ones. The admedian teeth are characterized by their finely denticulate free margins. The laterals are sickle-shaped, their edges being serrated in such a manner as to impart a feathery appearance to the tooth when that is turned over and seen in surface view.

The radula of *T. ungulina*, Linn. [Lovén, 6], differs only in a very slight degree from that of *T. communis*, Risso. The median tooth is sub-quadrate, it is wider at the base than the apex, and its cutting edge is finely denticulate.

T. rosea, Quoy & Gaimard, is described by Hutton [4] as follows:—"Length of central tooth rather more than half the breadth, the reflected portion finely denticulated on each side, and with a larger median cutting-point. First lateral [*admedian*] finely denticulated on the outer side; second lateral much broader than the third, and spoon-shaped at the tip; both are finely denticulated on the outer side."

T. australis, Lam. (Pl. VI, Fig. 7.) So far as I am aware, the radula of this species has not been previously figured. It is a very small and delicate structure, and closely resembles the radula of *T. communis*, Risso, the chief difference consisting in the shape of the median tooth, which has a somewhat convex base, its recurved apex tapers, rapidly ending in a fine median cusp, the lateral edges being finely serrated. The admedians are relatively large, the free margin is denticulate, terminating in a moderately large cusp. The lateral teeth are sickle-shaped, with finely serrated edges. Both *T. australis*, Lam., and *T. rosea*, Quoy & Gaim., are forms having a broad, shallow sinus in the outer lip of the shell; in this respect,

if the sinus has any connection with the slit in the Diotocardia, they may perhaps be considered slightly more primitive than *T. communis*. Their radulæ, however, are of the characteristic *Turritella* type, and show no trace of accessory lateral teeth.

T. triplicata, Broc. [Troschel, 9] (pl. xii, fig. 12). The most interesting feature in connection with the radula of this species is the presence of a third lateral tooth. This peculiarity, though not unique, is so unusual amongst the Tænioglossa as to suggest that it is a variation devoid of phylogenetic importance. The presence of an additional lateral tooth might, if borne out by other characters, suggest the retention of a primitive character and the approach to a rhipidoglossate type, yet, as we know nothing of the anatomy of this form, we can scarcely, from such slight evidence, regard *T. triplicata*, Broc., as being in any way more primitive than *T. communis*, Risso.[1]

The radulæ of the two following species of *Turritella*, belonging to the subsection *Mesalia*, Gray, differ considerably from that of *T. communis*, Risso They are characterized by the extreme elongation of the admedian and lateral teeth. In *T. lactea*, Möll. [Troschel, 9] (pl. xii, fig. 13), the median tooth has a broad concave base; the recurved cutting edge consists of a large rounded median cusp, with two smaller cusps on either side. The admedian and lateral teeth are entirely destitute of cusps or serrations, the recurved edges being quite smooth. *T. reticulata*, Migh. [Krause, 5] (pl. xvii, fig. 3), possesses an almost identical radula, the chief difference consisting in the denticulate character of the admedian and lateral teeth. According to Krause, this species possesses a small additional lateral tooth (rudimentary uncinus), comparable to the third lateral of *T. triplicata*, Broc.

Sars [8] (pl. vii, fig. 2) has figured the radula of *T. acicula*, Stimp. In this species there are only three teeth in a transverse row, the laterals being absent. The shape of the teeth is very singular; they are plate-like structures with strongly denticulate edges, differing from similar teeth in other species in that the margins are not reflexed. This type of radula is utterly unlike any occurring elsewhere amongst the Turritellidæ.

Genital organs. — The gonad of both sexes occupies the dorsal portion of the visceral mass; it is situated on the periphery of the coils, enclosing a central core of liver and bounding the posterior chamber of the stomach.

The male possesses neither penis nor accessory glands. The tubular testis connects with a convoluted vas-deferens, which runs

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[1] Since going to press, I have received, through the kindness of Miss Donald, several specimens of *T. triplicata*, Broc., from Naples. A microscopic examination of the radula failed to reveal the presence of an accessory lateral tooth, so that this species conforms to the typical tænioglossate condition. The general anatomy, so far as I have been able to make out from a cursory examination, appears to differ in no respect from that of *T. communis*, Risso. The otocyst contains a single otolith.

side by side with the rectum, and opens in the anterior portion of the mantle-cavity immediately above the genital groove (Pl. VI, Fig. 5, *g.g.*).

The female genital organs (Pl. VI, Fig. 2) are very similar; the ovary (*ov.*) gives origin to two fine ducts, which fuse to form the oviduct (*ov.d.*). On reaching the mantle-cavity, this structure becomes greatly enlarged, its walls take on a glandular character (*ov.d'.*), and eventually, after running parallel with the rectum for the greater part of its length, it opens into the anterior portion of the mantle-cavity. There is in addition a crescent-shaped accessory oviducal gland (*ov.g.*), communicating by means of a fine duct with the oviduct.

The most interesting structure in the anatomy of *Turritella* is a remarkably well-developed groove (Pl. VI, Fig. 2, *g.g.*) running along the floor of the mantle-cavity throughout its entire length; it is bounded on either side by fleshy ridges consisting of vacuolated tissue (Pl. VI, Fig. 5, *g.g*).

The groove lies close to the columella muscle (*c.m.*), and at its posterior extremity the two ridges enclosing it become free from the floor of the mantle-cavity (Pl. VI, Fig. 6, *g.g.*) and abut on the kidney (*k.*).

The cells lining the groove and sides of the ridges do not appear to be in any way specialized; some few of them are ciliated, but this ciliation is by no means a conspicuous feature. The anterior and extra-pallial portion of this structure is slightly modified; the ridge on the right side becomes vertically enlarged, and forms a very conspicuous fold, situated on the right side of the head and underneath the tentacle (Pl. VI, Fig. 1, *g.f.*). The ridge bounding the left side of the groove becomes much smaller, and finally disappears when it reaches the head of the animal. This groove, with its associated structures equally well developed, is present in both male and female specimens of *Turritella*.

In all probability one of its functions is, either to carry away, or receive, the genital products, for the openings of the vas-deferens and oviduct are situated almost immediately above it; it is, however, only the anterior portion that can be of use in this way, for the genital ducts open in the anterior region of the mantle-cavity quite close to its termination. What, then, can be the meaning of the extension of the groove to the extreme end of the mantle-cavity?

It is so conspicuous a structure that it must have some definite function. Its posterior end abuts on the kidney (Pl. VI, Fig. 6), and is near the aperture (*k.o.*), placing the excretory organ in communication with the mantle-cavity; it may therefore serve to carry away excretory products. In addition, it might serve to direct a current of water out of the mantle cavity, and so aid in respiration [Clarke, 2] (p. 332); any excretory products accumulated in the groove would at the same time be washed away by this stream of water. It seems strange that there should be a comparative scarcity of cilia on the epithelium of this structure, as the efficiency of maintaining a constant current of water down the groove would be greatly increased by the

presence of cilia. It may be that the absence of definite ciliation is due to imperfect preservation of the specimens, though the invariable presence of ciliated cells in the intestine, and the few that do occur in the groove, would seem to refute this suggestion.[1]

The presence of a spermatic groove is characteristic of many male Gastropods, e.g. Naticidæ, Cypræidæ, Strombidæ, etc. In these forms a penis is present, and the furrow, which is ciliated, leads directly from the aperture of the vas-deferens in the mantle-cavity to the penis. In *Spekia*, *Faunus*, and *Littorina* the structure is overhung by a flap or ridge [Moore, 7] (p. 171, pl. xv, figs. 1 and 11); in the latter form, and also in *Strombus*, a vestigial groove can be traced in the female.

Moore [7] (pp. 160 et seq., pl. xiv, figs. 10, 13) has described a remarkable structure in connection with the female genital organs of *Tanganyicia rufofilosa* and *Melania episcopalis*, Led. From the aperture of the oviduct a well-marked furrow runs forward on the right side of the body, and terminates in a little pit beneath the eye; this pit communicates with a brood-pouch, situated on the left side behind and below the tentacle in *Tanganyicia rufofilosa*, median and above the œsophagus in *Melania episcopalis*, Led. The furrow occupies the same position as does the spermatic groove in the male.

We have thus evidence of a genital groove occurring in both sexes of certain Gastropods. In all these forms the furrow has a definite connection with the genital aperture, and does not extend beyond it, whereas in *Turritella* the genital aperture is situated very far forward in the mantle-cavity, and, though it is placed just above the groove, yet has no such intimate connection with it as exists in any of the other aforementioned Gastropods. Moreover, the structure extends far beyond the genital aperture, to the extreme posterior end of the mantle-cavity.

There is no structure in *Littorina*, *Faunus*, etc., comparable to the well-marked extension of the groove which exists in *Turritella*, so that the homology of this structure is doubtful. The anterior portion and genital flap (Pl. VI, Fig. 1, *g.f.*) may, and in all probability do, correspond to the genital groove of *Littorina*, etc., but it is difficult to say what the remaining posterior portion can represent.

The *excretory organ* is fairly large, consisting of a characteristic spongy tissue (Pl. VI, Fig. 6, *k*); it opens directly into the mantle-cavity by means of a pore (*k.o.*), there being no long ureter. A reno-pericardial canal (*r.p.c.*) is present, placing the kidney in communication with the pericardium.

The *heart* and *pericardium* are those of a typical monotocardian. The ventricle gives origin to a common aorta, which almost immediately divides into anterior and posterior branches.

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[1] Since the above was written, I have received living specimens of *T. communis*, Risso, from Mr. E. W. L. Holt. Some of these were carefully fixed with corrosive sublimate in acetic acid, and an examination of transverse sections revealed the presence of definite ciliation of the epithelium of the genital groove. There appeared to be a special concentration of cilia near the apex of the outer ridge.

The *gill* (Pl. VI, Fig. 2, *g.*) is very large, extending throughout the whole of the mantle-cavity; the gill-filaments of which it is composed are exceptionally long, and are partially attached to the mantle, the unattached portion projecting freely into the mantle-cavity. The *osphradium* (*o.s.*) is a long rod-shaped body lying underneath the gill, and nearly coextensive with it; both gill and osphradium are very similar to those of *Cerithium*.

The floor of the mantle-cavity is beset with ridges which consist of glandular mucous-secreting tissue.

The nervous system.—Von Jhering [10] has figured and described the nervous system of *T. communis*, Risso, whilst Bouvier [1] has recently investigated that of *T. rosea*, Quoy & Gaim. I find that, though the description given by the former is accurate, yet his figure [10] (pl. x, fig. 5) is somewhat misleading, especially in respect to the relative size of the ganglia and length of the commissures.

The cerebral ganglia (*c.g.*) (Pl. VI, Figs. 3 and 4) are pyriform in shape, and are united to one another underneath by a short, broad commissure. The pleural ganglia (*pl.g.*, *pl'.g.*) lie slightly under, and are attached to the cerebrals by very short connectives. Two oval bodies, closely connect d to one another internally, are situated anteriorly and ventrally to the cerebrals; these are the pedal ganglia (*pd.g.*).

The cerebral and pleural ganglia are joined to the pedals by connectives, the pleuro-pedal being about twice as thick as the cerebro-pedal.

A visceral nerve is given off from the left pleural ganglion; it runs underneath the œsophagus towards the right side, passing into the sub-intestinal ganglion (*sb.g.*), which lies to one side of and slightly underneath the right pleural, and is joined to it by an extremely short connective (*z.*), the inter-visceral commissure of Von Jhering [10]; we have thus a condition of zygoneury on the right side.

The sub-intestinal ganglion, after giving off a pallial nerve (which almost immediately bifurcates, one branch innervating the upper part, the other the lower part of the mantle), is continued into the sub-intestinal branch of the visceral commissure, which, running parallel with the œsophagus to the end of the mantle-cavity, terminates in the abdominal ganglion (*ab.g.*). The right pleural ganglion gives off a visceral nerve that passes obliquely over the œsophagus and is continued into the supra-intestinal ganglion (*sp.g.*); from the latter the supra intestinal branch of the visceral commissure is given off; this runs beside the osphradium to the end of the mantle-cavity, and terminates in the abdominal ganglion.

From the left pleural ganglion a pallial nerve is given off to the mantle. The supra-intestinal ganglion gives origin to two branchial nerves, the anterior of which runs parallel to the left pallial nerve, and at the base of the mantle anastomoses with the latter by means of a very fine transverse commissure; hence on this side we have a condition of dialyneury (*d.*).

From the abdominal ganglion two nerves arise, the stouter of which innervates the genital gland. The following nerves are given off from the cerebral ganglion :—one, arising from the outer side of the ganglion, runs to the tentacle; close to this, and parallel with it, another very fine nerve can be distinguished which passes to the eye. The anterior portion of the ganglion gives origin to several nerves innervating the snout. The innermost of these runs along the side of the œsophagus, and at the junction of this structure with the buccal mass terminates in a large ganglion, situated immediately above the radula-sac. This buccal ganglion (*b.g.*) is connected to its fellow on the other side by a stout, broad commissure. From the under side of the cerebral ganglion a very fine nerve arises, which, passing between the cerebro-pedal and pleuro-pedal connectives, and crossing over the latter, supplies the otocyst (*ot.*). From the pedal ganglion several nerves are given off which pass to the anterior and posterior regions of the foot.

A slender nerve arises from the outer side of the pleuro-pedal connective, near the point where the auditory nerve crosses.

The *eyes* are situated at the base of the awl-shaped tentacles. Each consists of a closed cavity, the inner wall of which is densely pigmented, and contains a spherical lens.

The *otocysts* (Pl. VI, Fig. 4, *ot.*) approximate the posterior border of the pedal ganglia. Each encloses a single large circular otolith, which is striated both concentrically and radially.

In *T. rosea*, Quoy & Gaim., Bouvier [1] (p. 201) describes the presence of several small rectangular otoconia in the otocyst, in addition to a large circular otolith; he does not seem to attach much importance to this interesting condition, nor to the difference between the two species *T. communis*, Risso, and *T. rosea*, Quoy & Gaim., in this respect. The presence of otoconia is generally regarded as a primitive feature, and is characteristic of the majority of the Diotocardia and Architænioglossa, whilst the single otolith is indicative of a higher degree of organization, and occurs in many of the Monotocardia, notably in those forms which, on other grounds, have been regarded as specialized, e.g. the Rachiglossa, Toxoglossa, and several of the Tænioglossa.

Whether the presence of both otolith and otoconia in the otocyst of *T. rosea*, Quoy & Gaim., and of only an otolith in *T. communis*, Risso, indicates that the former species is more primitive than the latter, is problematical; but it would certainly be interesting to see if these differences exist in other species of *Turritella*.[1]

A similar condition obtains in forms other than the Turritellidæ. *Vivipara vivipara* (Linn.) possesses otoconia, whilst a single otolith occurs in *Bithynia tentaculata*, Linn. *Melania amarula*, Linn., and *M. tuberculata*, Müll. (and its variety *M. costata*), have otoliths; *M. filocarinata*, Mous., and *M. asperata*, Lam., have otoconia [1] (pp. 419, 420).

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[1] It is interesting to note, as previously mentioned (p. 58), that *T. rosea*, Quoy & Gaim., is a form in which the outer lip possesses a broad, shallow sinus, and would in this respect seem to be more primitive than *T. communis*, Risso, in which the outer lip is entire.

The Turritellidæ are undoubtedly, as maintained by Bouvier [1], closely approximated to the Cerithiidæ. The nervous system of *T. communis*, Risso, presents points of agreement with that of *Ceratoptilus* [1] (p. 146, pl. viii, fig. 33) in some respects, and with *Telescopium* [1] (p. 145, pl. viii, fig. 32) in others. That is, it resembles the nervous system of the zygoneurous Cerithiidæ more nearly than that of any other prosobranch. There are other points of structural similarity between *Cerithium* and *Turritella* besides those of the nervous system, as, for instance, the peculiar form of the gill and the elongate osphradium. *Turritella*, though in no way particularly specialized, can scarcely be regarded as approaching a primitive type; it certainly presents a few characters that may be considered somewhat primitive, as, for example, the presence of an epipodium, also the peculiar papillæ and fringe of the mantle, and, in the case of *T. rosea*, Quoy & Gaim., the presence of otoconia; yet, taken on the whole, and especially with reference to the nervous system, we must look upon *Turritella* as a moderately highly organized monotocardian, and presenting no approach to the structure of the Diotocardia. If the notched forms of *Turritella* are, as is supposed, allied to the extinct genus *Murchisonia*, they will have to be removed from the family Turritellidæ. Before this point can be cleared up, however, we must have some knowledge of the anatomy of these forms.

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